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Cooperation

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Cooperation, defined as an action in which an individual incurs a cost to benefit others, is seen in many human activities such as food sharing, childcare, infrastructure building, resource defense, and warfare. Cooperation presents an evolutionary conundrum because helping someone at a personal cost lowers the helper's fitness—ability to transmit their genes to subsequent generations—and therefore should be disfavored by natural selection. Theories of the evolution of cooperation aim to identify distinct mechanisms by which cooperators, while incurring a temporary cost, accrue more benefits in the long run than defectors—individuals who receive the benefit but do not themselves incur the cost of cooperating. Theoretical models, constructed via mathematics and simulations, compare how cooperators and defectors perform under different scenarios, generating predictions about how cooperation can arise and persist. These models inform field observations or laboratory experiments that explore the cognitive biases and psychological preferences that drive cooperation in the real world. These complementary approaches have helped identify a range of behavioral strategies, supported by corresponding cognitive capacities, by which cooperation can be sustained. A key question in the field is why humans cooperate more than other animals, including in large groups and in transient interactions with strangers.

History

The modern study of cooperation from an evolutionary perspective began with the publication of William Hamilton's seminal theory of *kin selection* ([Hamilton, 1964](#)). Even before Hamilton, notable scholars such as Charles Darwin and population geneticist J.B.S. Haldane were intrigued by the phenomenon of cooperation and verbally articulated their intuitions on how cooperation could provide competitive advantages. However, Hamilton presented the first mathematically grounded theory by demonstrating that individuals can maximize their fitness by helping genetic relatives if the cost to self is lower than the benefit to the recipient, weighted by how closely related the two individuals are. In the decades following Hamilton's publication, additional mechanisms by which cooperation can evolve were identified. Robert Trivers posited the theory of *reciprocal altruism* ([Trivers, 1971](#)), Richard Alexander extended the intuitions from direct reciprocity to posit the theory of *indirect reciprocity* ([Alexander, 1987](#)), and Robert Boyd and Peter Richerson developed the idea of *cultural group selection* as part of their theorizing of cultural transmission ([Boyd and Richerson, 1985](#)) [see [Social Learning](#)]. These theories highlighted behavioral strategies for cooperation that are evolutionarily viable and helped generate predictions about the cognitive capacities required to make decisions and perform behaviors that correspond with the strategies.

Core concepts

Kin selection theory

Kin selection theory posits that by helping those who share a recent common ancestor, a cooperator is more likely to be helping someone who is also a cooperator, thereby excluding defectors from the benefits of

cooperation ([Hamilton, 1964](#)). It predicts that there will be cognitive capacities that have evolved for recognizing one's close kin and emotions such as love towards our close kin that motivate us to be attentive to their needs and care for them ([Hames, 2015](#)) [see [Foundations of Emotion](#)].

Reciprocity theory

Reciprocity theory posits that when two individuals interact repeatedly, an individual can minimize the risk of exploitation and accrue long-term benefits by conditioning their behavior on whether their partner previously cooperated or not ([Axelrod, 2012](#)).

Indirect reciprocity theory

Indirect reciprocity theory posits that cooperators can exclude defectors from the benefits of social exchange by conditioning cooperation on how recipients treated others in the past, thereby facilitating community-level cooperation and motivating humans to care about their public reputation ([Nowak & Sigmund, 2005](#)).

Third-party punishment theory

Third-party punishment theory posits that direct costs are imposed on defectors through punitive actions dispensed by unaffected observers (third-party punishment), which can help explain why we cooperate even in large groups, with unfamiliar individuals, and in transient interactions ([Boyd et al., 2003](#)).

Norm enforcement

Indirect reciprocity and third-party punishment are important mechanisms by which humans enforce social norms—common expected standards of behavior within a society [see [Normativity](#)]. Norm enforcement allows for cooperation and defection to be specified by complex sets of rules and for groups to have different cooperative behaviors.

Cultural group selection

Groups with cultural traits—norms, beliefs, practices, and technology—that enhance within-group cooperation (e.g., norms that promote helping, or prohibit harming, comembers) can outcompete groups that are less cooperative. In this way, cooperative groups can expand their territory and grow their population, leading to the spread of their cooperative way of life ([Boyd et al., 2011](#)).

Questions, controversies, and new developments

Could seemingly cooperative acts be selfishness in disguise?

It is hard to measure the cost and benefit to actor and recipient in real-world cooperation. Therefore, it is often unclear whether cooperative actions may in fact provide immediate benefits to the actor, which would obviate the need to deter free riders. Immediate benefits could arise from improved social coordination, gaining an

edge in competitive partner choice, or by signaling desirable qualities ([Archetti et al., 2011](#); [Barclay et al., 2021](#)).

Is cooperating with strangers an evolutionary mistake?

Some researchers contend that human cooperation in transient interactions with strangers is not an evolved adaptation but an ancestral cooperative psychology for small-scale cooperation misfiring in contemporary novel environments ([Krasnow et al., 2013](#)). This debate fuels questions about the social structure of hunter–gatherer societies ([Padilla-Iglesias et al., 2022](#)).

Do we need group-level selection to explain human cooperation?

Whether cultural group selection is needed to explain human cooperation is keenly debated ([Richerson et al., 2016](#); [Smith, 2020](#)). One area of contention is whether human populations are structured into groups that are sufficiently different in their cultural traits for group-level competition to be an important evolutionary force. Another is whether group-level selection is needed for cooperative norms to spread or whether such norms can arise and spread through self-interest.

Broader connections

Although the above summary focuses on evolutionary explanations of cooperation, empirical studies from different disciplines have highlighted the cognitive and physiological underpinnings of cooperation. Psychologists have examined the development of cognitive capacities needed for human cooperation such as language, theory of mind, joint attention, inequality aversion, and morality ([McAuliffe et al., 2017](#)) [see [Language](#); [Theory of Mind](#)]. The field of behavioral economics documents human decision-making under various self-versus-other benefiting scenarios, helping to identify human social preferences and evaluate theories of cooperation ([Thaler, 2016](#)). Cross-cultural work in anthropology and psychology helps assess to what extent cooperation is driven by culturally transmitted social norms versus universal behavioral predispositions ([Henrich et al., 2006](#)). Comparative studies of nonhuman primates identify the derived versus ancestral features of human cognition and their relevance to the taxonomic distribution of cooperation ([De Petrillo & Rosati, 2021](#)). Studies of cooperation in small-scale societies are essential to piece together key features of human life history, diet, reproductive behavior, and health ([Fox et al., 2022](#); [Ross et al., 2023](#)).

Artificial intelligence disclosure

ChatGPT 5 was used to edit the prose to improve clarity and conciseness. Original content was generated by the author, and all generative artificial intelligence edits were checked by the author for accuracy.

Further reading

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